

# Temperature Relations of Puget Sound Thais in Reference to Their Intertidal Distribution

BY

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(9 Text figures)

## INTRODUCTION

TEMPERATURE IS GENERALLY considered to be an important factor in governing the upper limit of the vertical distribution of intertidal organisms (NEWELL, 1970). The tides create an emersion stress period, which increases with increasing beach elevation for intertidal organisms. Therefore, the vertical position of an organism in the intertidal zone determines the amount of temperature stress to which it is exposed while emerged. Many studies have shown that correlations exist between a species' vertical tidal height and its response to temperature in terms of lethal thermal limits (FRAENKEL, 1960; MICALLEF, 1966), the temperature independence of the metabolic rate (NEWELL, 1969; DAVIES, 1966), and the rate of feeding (MORTON, BONEY & CORNER, 1957).

WOLCOTT (1973) has advanced the hypothesis that in general, the range limits of animal populations are not directly limited by physical factors, but by behavior, competition, or other biotic factors, and that interspecific differences in adaptation to physical stress do not create, but allow for, the vertical distribution and partitioning of the intertidal environment. This would appear to account for the fact that the lethal thermal limits of intertidal animals are usually considerably higher than the temperatures experienced in their habitat (HARDIN, 1968). But since temperature is known to affect the normal functioning of organisms at sublethal temperatures, *e.g.*, feeding and reproduction in *Thais lapillus* (LARGEN, 1966), the temperature variations which occur within an organism's intertidal range potentially could affect the competitive or reproductive ability, or both, of organisms within their habitats. Therefore an organism's position in the intertidal area, by determining the regime of physical stresses to which it is exposed, could vary competitive ability within its range and influence the consequential zonation of the species.

Many intertidal gastropods have been shown to exhibit intraspecific shore-level size gradients in their natural environment (VERMEIJ, 1972). Two patterns are commonly found (VERMEIJ, *op. cit.*): 1) shell size tends to increase in an upshore direction in gastropods characteristically found in the upper intertidal zone, and 2) shell size decreases with increased tidal height in lower intertidal gastropods. It has been suggested that the size gradients found in high intertidal gastropods result from limiting physical stresses in the upper intertidal region (VERMEIJ, *op. cit.*). This places the larger individuals of a population, which by surface area to volume ratio considerations should be best suited to deal with temperature and desiccation stress, at the top of the species' vertical range. Higher tolerance levels in larger individuals of populations displaying this size gradient pattern have been shown to exist (HARDIN, 1968; DAVIES, 1969; EDWARDS, 1969). The size gradient patterns found in lower intertidal gastropods are thought to result from biotic factors (VERMEIJ, *op. cit.*). Since this size gradient pattern places the smaller snails in the more physically stressful portion of the population's vertical range, by surface area to volume ratio considerations, it is placing the least tolerant members of the populations in the most stressful portion of the species' vertical range (VERMEIJ, *op. cit.*). But, even if this size gradient phenomenon results from the biotic stresses of the lower intertidal zone which would be more severe on the smaller members of a population, the apparent non-adaptive placement of the smaller individuals in the most physically stressful habitat, could suggest a cause for intraspecific physiological adaptations. To our knowledge no work has been done to shed light on this question.

In the Puget Sound area both *Thais lamellosa* (Gmelin, 1791) and *Th. emarginata* (Deshayes, 1839) populations exhibit shore-level size gradients with the smaller juvenile snails found at the top of each species' vertical range

(BERTNESS, 1976). In addition, the *Th. emarginata* population is found at higher intertidal levels than *Th. lamellosa* (CONNELL, 1970; BERTNESS, *op. cit.*). It has also been shown that the intra- and interspecific zonation patterns exhibited by these snails result from behavioral responses to the continuous gradients of light and elevation found in the intertidal area (BERTNESS, *op. cit.*), so that physical stresses do not directly regulate the species' distribution.

The purpose of this investigation is to determine if *Thais lamellosa* and *Th. emarginata* populations are intra- and interspecifically adapted to their natural zonation patterns in terms of temperature stress. To achieve this end, the snails' lethal thermal limits are investigated as well as their activity and metabolic rate responses to temperature fluctuations.

## METHODS

### Lethal Thermal Limits

Since the thaidis are only exposed to extreme temperature conditions while exposed during a low tide, the lethal thermal limit determinations were made only on emerged snails. Determinations were made for a large and a small size class of *Thais lamellosa* and a mixed size group of *Th. emarginata* under humidity conditions of 100% and 0% relative humidity in August, 1974. The organisms used in the experiments were all collected at Baker's Reef, Lummi Island, Washington (48°40'N; 122°41'W) and were starved and acclimated to 13 - 15°C in aerated seawater for at least 72 hours before use. After dividing the snails into distinct size class/species groups, the shell lengths were determined (from apex to siphonal canal) with vernier calipers.

In the experimental procedure, individual organisms were submerged in 125 ml vented vials in batches of 10 vials in a constant temperature bath ( $\pm 1^\circ\text{C}$ ) for a predetermined interval of time. Pretests were made to determine the approximate times of thermal death from 29 to 35°C for each group under both wet and dry conditions. The humidity of the vials was controlled by adding 2 ml of fresh seawater for the 100% relative humidity condition, and a small crucible (04, Coors) filled with fresh CaSO<sub>4</sub> (Drierite) for the 0% relative humidity condition. This method of determining lethal thermal limits is essentially identical with that described by FRAENKEL (1960).

Since thaidis are slow-moving organisms and go into a comatose state under stress (SANDISON, 1968), the batches of 10 snails were run at each predetermined temperature/

time interval and then given 24 hours to recover. The recoveries were run at the acclimation temperature in large finger bowls with the thaidis upside down and completely submerged in fresh, aerated seawater. After the recovery time the condition of each snail was determined by poking its foot with a seeker and scoring its condition using the following point system (after GIBSON, 1970).

- 2 = Active or fully recovered. Either the foot is attached or is exposed but very responsive to seeker.
- 1 = Moribund. Foot is exposed but slow in reacting to seeker probe.
- 0 = Dead. Either the foot is exposed, but does not respond to seeker, or operculum is tightly closed and shows no response.

Using this point system, where batch scores of 20, 10, and 0 correspond to 0%, 50%, and 100% mortality respectively, the scores were readily converted to percent mortality. The raw data were then subjected to probit analysis (FINNEY, 1971) which gave LD50 estimates with confidence intervals and analysis of variance on the probit line fit.

Field measurements of humidity and temperature were made with an Atkins psychrometer and a Wheatstone bridge thermister unit respectively. Both parameters were measured within 5 cm of the substrate to accurately reflect the conditions in the snails' habitat. Snail tissue temperatures were taken by inserting a thermister mounted in a hypodermic needle into the foot of the snail. All air temperature measurements were taken in the shade to avoid radiation interference. Tidal heights were determined by methods essentially identical with those described by DAYTON (1971) and were found to be accurate to  $\pm 8$  cm.

### Metabolic Rates

Emerged and submerged respiratory rates of large and small size classes of both *Thais lamellosa* (June, 1974) and *Th. emarginata* (October, 1974) were taken over a 0 - 30°C range. The *Th. lamellosa* and *Th. emarginata* used in these experiments were collected near Anacortes, Washington at the Shannon Point Marine Center (48°29'N; 122°45'W) and Washington Park West Beach (48°31'N; 122°42'W), respectively. The snails were all acclimated and starved for at least 48 hours and no longer than 7 days in 13 - 15°C aerated fresh seawater before use in the experiments. Algal epiphytes and barnacles were removed from the shells before use. All snails were towel-dried and weighed to the nearest milligram after each experiment, were used only once, and returned to the beach.

Oxygen consumption is expressed in microliters ( $\mu\text{l}$ ) of oxygen (STP) per hour per gram of wet tissue. To determine the tissue weight of the experimental organisms, 30 snails of all sizes and each species were towel-dried and weighed to 0.001 grams. The snails were then oven dried for 6 hours at 100°C. Following drying, the shells were cracked and the dry tissue was removed. The shells were then weighed (to 0.001 grams) and the wet tissue weights were calculated. The tissue weight (Y) and whole wet weight (X) were then subjected to regression analysis. A significant relationship ( $P < 0.01$ , ANOVA) was found for both *Thais emarginata* ( $Y = 0.397X + 0.0042$ ) and *Th. lamellosa* ( $Y = 0.215X + 0.1181$ ), and these relationships were used to convert the whole wet weights of the experimental organisms to wet tissue weights.

Since the size class data from field observations (BERTNESS, 1976) were in shell lengths, it was necessary to determine if there is a significant relationship between shell length and whole wet weight, which would make the results comparable. Fifty snails of each species and of all sizes were measured with calipers (from apex to siphonal canal) to 0.01 cm, towel-dried, and weighed to 0.001 gms. The relationship between shell length (X) and whole wet weight (Y) for both *Thais emarginata* ( $Y = 1.934X - 3.412$ ) and *Th. lamellosa* ( $Y = 5.589X - 12.770$ ) was found to be significant ( $P < 0.05$ , ANOVA).

A Gilson differential respirometer was used to determine the emerged oxygen consumption of the snails. Standard techniques for the respirometer (UMBRETT, BURRIS & STAUFFER, 1964) were followed. For each run the snails were placed in the respirometer flasks (one to a flask) and allowed to attach to the bottom. The smaller snails, *Thais emarginata* and the small size class of *Th. lamellosa* were run in 10 ml flasks, while the large *Th. lamellosa* were run in 100 ml flasks. The flasks were then allowed to thermally equilibrate to the bath for 50 minutes before the run was initiated. The runs lasted 3 hours each, with oxygen consumption readings taken at 30 minute intervals. Determinations were made for each size class/species group at 5°C intervals from 0 to 30°C.

Submerged oxygen consumption was measured using a galvanic cell oxygen analyzer (MANCY & WESTGARTH, 1961) in a closed respirometer system designed by one of us (D. E. S.). The oxygen electrode is incorporated with an air-tight stirring unit in a rubber stopper fitted to an appropriate flask which acts as the respirometer chamber. A similar apparatus has been described by MANCY & WESTGARTH (*op. cit.*).

For each run four 125 ml respirometers were filled with air-saturated and thermally equilibrated seawater,

the weighed snails were lowered into the chambers, allowed to attach, and the thermally equilibrated electrode units were inserted. The respirometers were then lowered into a temperature controlled ( $\pm 0.1^\circ\text{C}$ ) water bath on clamps and run for 150 minutes, taking readings of electrode output every 30 minutes. Five runs were made for each size class/species group at 10°C intervals from 0 to 30°C.

Oxygen consumption is calculated as described by MANCY & WESTGARTH (1961) using the seawater oxygen saturation values given by GREEN & CARRITT (1967). Salinity determinations were made on a Fiske research osmometer.

In order to compare the different size classes of thaidis under all conditions, the respiration of the size classes were all corrected to a specific weight using the formula:

$$Z = \log O_2 + (b-1)(\log W - \log X)$$

where W is the desired weight, X is the original wet tissue weight, and  $b-1$  is the weight-specific regression coefficient of the weight-rate power function (ROBERTS, 1957). These calculations were run on both species of snails at each tested temperature and running condition. The power function regression equations were subjected to covariant analysis, and the species-temperature groups which did not differ significantly from the total pooled regression were pooled, and a separate regression was calculated to describe their weight-rate power function. The corrected weights used were:

Large <i>Thais emarginata</i>	1.010 grams
Small <i>Thais emarginata</i>	0.323 grams
Large <i>Thais lamellosa</i>	2.900 grams
Small <i>Thais lamellosa</i>	0.243 grams

which represent the calculated means of the large and small *Thais* sp. wet tissue weights.

Analysis of variance was performed on the resulting size class Z values over the 0-30°C range for both emerged and submerged rates to determine the effect of temperature on the rates.

### Activity

The rate of crawling of the thaidis was determined under both emerged and submerged conditions over a 0-30°C range at 5°C intervals. Both large and small size classes of *Thais lamellosa* and a mixed size class of *Th. emarginata* were run in August, 1974.

All of the snails used in the experiments were collected at the Shannon Point Marine Center and were acclimated for 72 hours prior to testing in 15°C fresh aerated seawater. The snails were each measured to 0.01 cm (from apex to siphonal canal) with vernier calipers before use,

and used in only one run each and then returned to the beach.

Submerged activity was measured in a temperature controlled ( $\pm 0.1^\circ\text{C}$ ) 79 x 64 x 16 cm tank filled to a depth of 8 cm with fresh seawater. The bottom of the tank was marked with a 1 cm square grid. At the beginning of each run 10 numbered (snails were all given grease pencil numbers) snails were placed in the tank and their positions were recorded. Each run lasted 120 minutes and at 30-minute intervals the snails' new coordinates were noted and the distance moved was calculated. Two separate runs were made for each size class/species group at each temperature.

The emerged activity was measured on 50 x 40 cm glass plates, marked with a 1 cm square grid, and placed in an incubator. The same measuring technique was used as in the submerged activity tests. Temperature fluctuations in the incubators, which occurred while new positions were recorded, were  $\pm 3^\circ\text{C}$  and of short duration.

Both emerged and submerged tests were made under artificial light and all results were converted to centimeters per hour and subjected to analysis of variance.

## RESULTS AND DISCUSSION

### Lethal Thermal Limits

The probit line fit for each species/size class group under all experimental conditions was found to be significant ( $P < 0.001$ , ANOVA). Statistical testing between temperature groups was limited to 95% confidence interval comparisons due to the probit analysis technique employed (FINNEY, 1971).

The LD50 values found for the 3 groups tested under conditions of 100% relative humidity are shown in Figure 1. *Thais emarginata* shows significantly higher thermal limits than either *Th. lamellosa* size class at each comparable test temperature. This correlates with their intertidal zonation differences (CONNELL, 1970). Within the *Th. lamellosa* size classes under wet conditions (Figure 1) at each temperature, there is a trend for the small snails to be more tolerant. This corresponds to the intraspecific size distribution within the species, but differences are not significant, with one exception ( $29^\circ\text{C}$ ).

In an effort to ascertain the effect of low humidity on the lethal thermal limits of the snails, tests identical to those made at 100% relative humidity were made at 0% relative humidity. Both species and size classes of *Thais lamellosa* showed significantly longer LD50 times under the dry condition (Figure 2) when compared with

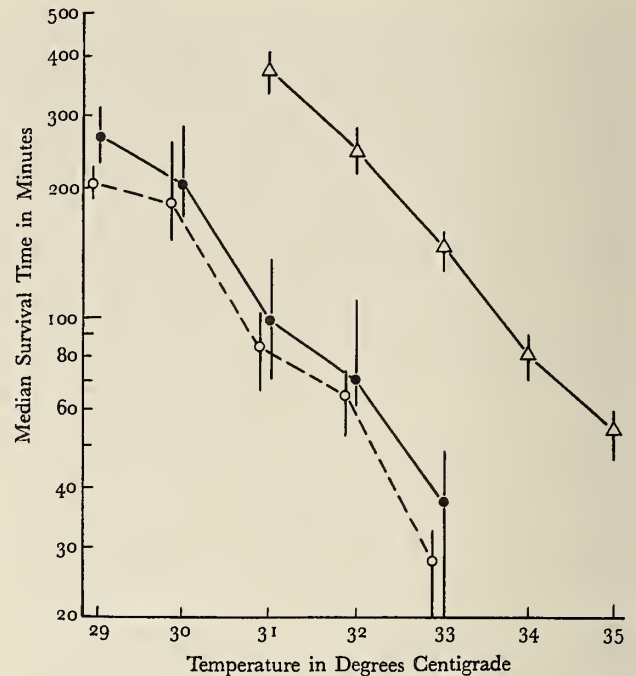


Figure 1

LD50 values under 100% relative humidity conditions for *Thais emarginata* ( $\Delta$ , mean shell length  $2.32 \pm 0.121$  (SD) cm), a small size class ( $\bullet$ ) of *Thais lamellosa* (mean shell length  $2.23 \pm 0.529$  (SD) cm), and a large size class ( $\circ$ ) of *Thais lamellosa* (mean shell length  $4.05 \pm 0.506$  (SD) cm). Vertical bars indicate 95% confidence intervals

results for the 100% relative humidity tests (Figure 1). This is what would be expected due to the facilitation of evaporative cooling with lower humidity (PROSSER, 1973). In addition, under dry conditions the small *Th. lamellosa* size class showed significantly greater LD50 values than the larger *Th. lamellosa* (Figure 2). Evaporative cooling would appear to play a potentially important role in the thermal relations of the thaidis.

The percentage survival increase from wet to dry conditions at each temperature was calculated for the 2 *Thais lamellosa* size classes using the data presented in Figures 1 and 2. A trend ( $P < 0.10$ , paired t-test) was found between the percent survival increase of the small *Th. lamellosa* ( $\bar{X} = 119.6\%$ ) and the large size class ( $\bar{X} = 85.5\%$ ). Based on surface area to volume ratios of large and small snails, one would expect the small *Th. lamellosa*

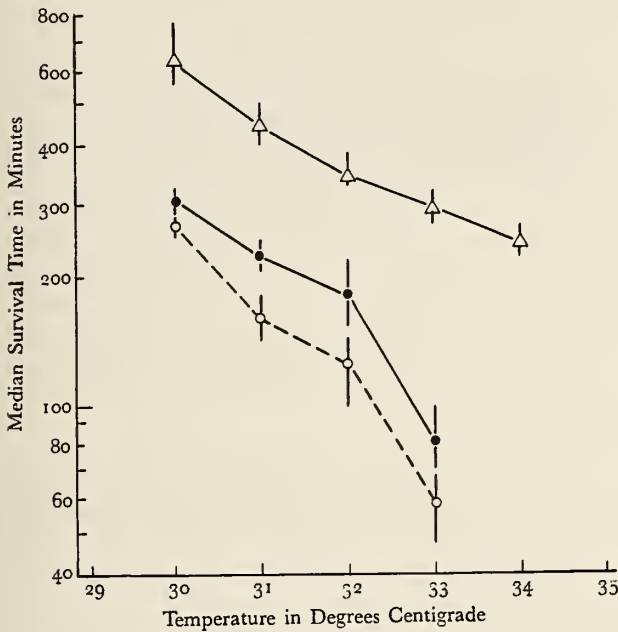


Figure 2

LD<sub>50</sub> values under 0% relative humidity for *Thais emarginata* (Δ, mean shell length  $2.32 \pm 0.121$  (SD) cm), small size class (●) of *Thais lamellosa* (mean shell length  $2.42 \pm 0.421$  (SD) cm) and a large size class (○) of *Thais lamellosa* (mean shell length  $4.00 \pm 0.364$  (SD) cm). Vertical bars indicate 95% confidence intervals

to be the most vulnerable to high environmental temperatures. These data indicate that evaporative cooling in the smaller snails is a more efficient cooling mechanism and a plausible explanation for their higher thermal limits. The interaction between temperature and humidity in determining the lethal limits of intertidal organisms has been stressed by other researchers (KENSLE, 1967; WOLCOTT, 1973).

Previous research has demonstrated that generally the thermal tolerances of intertidal organisms considerably exceeds the temperatures to which the animals are exposed in their environment (HARDIN, 1968; WOLCOTT, 1973). Field measurements of thaid tissue temperatures and habitat temperatures (Figure 3) appear to verify this finding for the thaid, since both snail and habitat temperatures are considerably lower than the temperatures required to cause mortality within the period of time that the animals would be exposed to the air (Figures 1 and 2). However, these data (Figure 3) were col-

lected during a midmorning fall low tide and therefore do not represent the maximum temperatures experienced by the snails during the summer.

The tissue temperature of the snails is consistently higher than the ambient air temperature in the snails' microenvironment (Figure 3). This observation is in accord with LEWIS' (1963) work with intertidal gastropods, the temperature difference being attributed to solar radiation. From this it would seem unreasonable to predict the exposure of organisms to lethal temperatures on the basis of environmental temperatures alone. Furthermore,

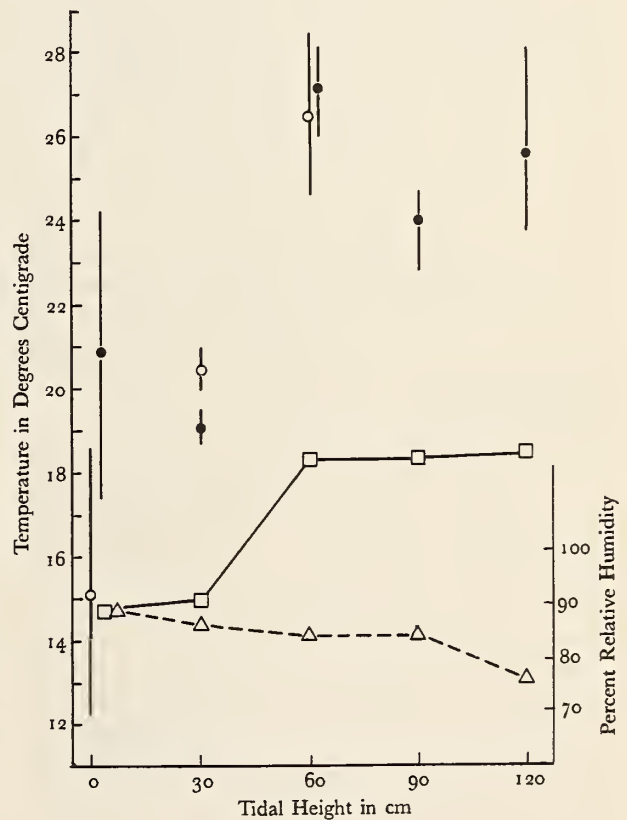


Figure 3

Tissue temperatures of *Thais lamellosa* (○) and *Thais emarginata* (●) found at different tidal heights at Washington Park, September 14, 1974, during a -6 cm low tide. Values represent the mean of at least 5 snails, and the vertical bars indicate the tissue temperature range. The ambient air temperatures (□) and relative humidities (Δ) in the thaid's microhabitat (5 cm above the rock surface) are also given

the effect of lethal temperatures on populations cannot be estimated by comparing the temperatures necessary to cause mortality in 50% of a population to the exposure temperatures. In actuality, mortalities of much smaller magnitude, which would be caused by lower temperatures and exposure times, could be important factors in the natural population distributions.

The results in Figure 3 also demonstrate the effect of tidal height on the physical parameters of temperature and humidity during a low tide. Both snail tissue temperature and the temperature in the snails' habitat show general increases with increased tidal height. The humidity, however, shows a constant decrease with tidal height. This could mean that although the snails in the upper intertidal area are exposed to higher temperatures, the lower humidity would allow them to evaporatively cool more efficiently. The inconsistency seen in the increase in *Thais emarginata* tissue temperature with tidal height (Figure 3) was unexpected. Since temperature did not show any drastic increase above the 60cm tidal height, whereas humidity decreases, evaporative cooling could be responsible for this trend. More realistically, however, snails from the upper intertidal zone are generally found in more protected habitats than the snails from lower tidal levels (personal observation), so that even though an effort was made to select "exposed" snails for the measurements, the observed variability could be due to habitat differences between the tidal levels.

SANDISON (1968) has suggested that lethal thermal limits are only indirectly responsible for limiting gastropod species upper intertidal distribution; the actual limiting factor being the heat coma of the organisms involved, which can occur up to 10° C lower for any particular LD50 time (SANDISON, *op. cit.*). Coma could be responsible for the ecological death of a snail, since in most organisms (including the thaidis) the animal loses its grip on the substrate and can be washed by the tide into a hostile and drastically different environment. We have observed apparent heat coma in both *Thais lamellosa* and *Th. emarginata* in the field and have recorded minimum tissue temperatures of 26.8° C and 31.2° C respectively in the immobilized snails. The decision to regard a snail found in the field to be in heat coma was a subjective one and was based on 2 criteria: 1) the snail had lost its grip on the substrate and was very slow to react to touching its foot; and 2) the snail was in an exposed position and the snails in more protected locations were still firmly attached to the substrate. In addition, thaidis judged to be in heat coma were found infrequently, with their occurrence coinciding with hot days and spring low tides (personal observation). The tissue temperatures found for heat coma thaidis when compared with the

tissue temperatures found at different intertidal heights (Figure 3) suggest that heat coma could be limiting the upper vertical distribution of both thaidis under consideration. Even if coma does not cause ecological death by directly moving the snails into different habitats, by virtue of immobilizing the animal it could affect its activities and consequently its competitive ability. Further work will be needed to test this, however, including the determination of LD50 values using an ecological death rather than a physiological death criterion, in addition to verifying the ecological fate of a moribund thaid. If thermal limits do indeed affect the vertical distribution of the thaidis, they would appear to reinforce the zonation patterns that are established and maintained by behavioral means (BERTNESS, 1976).

An interesting difference was noted in the behavior of *Thais lamellosa* and *Th. emarginata* on entering heat coma, both in the laboratory and in the field. On entering coma, *Th. lamellosa* withdraws completely into its shell and tightly closes the operculum. *Thais emarginata*, in contrast, usually leaves its foot exposed and occasionally extends its foot out further when going into heat coma. This behavior by the higher intertidal *Th. emarginata* on reaching near-lethal temperatures could represent a response to enhance cooling. This would be possible because of the larger surface area available for evaporative cooling, as well as the exposure of the foot to the cooler ambient air (Figure 3).

### Oxygen Consumption

Metabolic rate was chosen as an indicator of internal state during environmental change, since it reflects the sum total of the energy transformation taking place in an organism. It is possible, however, that alternate anaerobic pathways may act to confound this picture (HAMMEN, 1969; HOCHACHKA & MUSTAFA, 1972). In addition, recent studies (summarized by NEWELL, 1969) have shown that many intertidal organisms display a temperature independent resting metabolism as an adaptation to the fluctuating intertidal environment.

The weight regression equations for both *Thais lamellosa* and *Th. emarginata* under submerged (Table 1) and emerged (Table 2) conditions were subjected to covariant analysis by species and conditions of the experiment (submerged and emerged). Both species showed a significantly greater ( $P < 0.05$ ) regression coefficient when emerged. Under both submerged and emerged conditions, the 2 thaidis showed pooled (combined temperature groups) regression coefficients that did not differ significantly. Therefore, in both species the respiratory rate is propor-

Table 1

Weight (X) — rate (Y) regression equations for the submerged respiration of *Thais lamellosa* and *Thais emarginata* at four different temperatures. Asterisks indicate regressions that differ significantly ( $p < 0.05$ , ANCOVA) from the others within each species

Species and Temperature °C	Number in Sample	Regression Equation	95% Confidence Interval on $\hat{Y}$
<i>Thais lamellosa</i>			
0	17	$Y = 0.189X + 1.790$	$\pm 0.1435$
10	20	$Y = 0.128X + 2.133$	$\pm 0.1170$
20	20	$Y = -0.11 X + 1.653$	$\pm 0.0899$
30	15	$Y = 0.760X + 1.674^*$	$\pm 0.1955$
<i>Thais emarginata</i>			
0	20	$Y = 0.065X + 1.877$	$\pm 0.0606$
10	20	$Y = -0.562X + 1.875^*$	$\pm 0.1170$
20	20	$Y = -0.080X + 1.853$	$\pm 0.0857$
30	21	$Y = 0.073X + 1.946$	$\pm 0.0893$

Table 2

Weight (X) — rate (Y) regression equations for the emerged respiration of *Thais lamellosa* and *Thais emarginata* at seven temperatures. Asterisks indicate regressions that differ significantly ( $p < 0.05$ , ANCOVA) from the others within each species.

Species and Temperature °C	Number in Sample	Regression Equation	95% Confidence Interval on $\hat{Y}$
<i>Thais lamellosa</i>			
0	36	$Y = 0.502X + 0.823$	$\pm 0.1157$
5	36	$Y = 0.568X + 1.230$	$\pm 0.1111$
10	35	$Y = 0.499X + 1.504$	$\pm 0.1030$
15	36	$Y = 0.333X + 1.195$	$\pm 0.0969$
20	35	$Y = 0.476X + 1.57$	$\pm 0.1011$
25	36	$Y = 0.576X + 1.390$	$\pm 0.1238$
30	36	$Y = 1.101X + 1.315^*$	$\pm 0.1818$
<i>Thais emarginata</i>			
0	33	$Y = 0.642X + 0.802$	$\pm 0.1068$
5	36	$Y = 0.907X + 1.215^*$	$\pm 0.1183$
10	35	$Y = 0.780X + 1.469$	$\pm 0.1111$
15	33	$Y = 1.418X + 1.359^*$	$\pm 0.1838$
20	32	$Y = 0.589X + 1.384$	$\pm 0.1414$
25	49	$Y = 0.544X + 0.960$	$\pm 0.1273$
30	34	$Y = 0.613X + 1.360$	$\pm 0.1131$

tional to the power,  $-0.068$  of the wet tissue weight while submerged, and  $+0.687$  while emerged. The emerged power function is in close agreement with HEMMINGEN'S (1960) conclusion that in poikilothermic animals as a whole, respiration is proportional to the power  $0.75 \pm 0.015$  of body weight. The submerged power function, however, is not significantly ( $P < 0.01$ ) greater than zero

and is therefore not easily explained, since it refutes the weight-rate relationship usually found in organism metabolism. Since the thaidis show their highest activity while submerged (CONNELL, 1970), activity differences between the snail sizes could possibly account for this lack of rate-weight relationship. But data presented later in this paper (Figure 8) will show that the smaller snails

are more active while submerged than the larger thaid, a situation which would appear to have an accentuating effect on the normally observed higher metabolic rate in smaller individuals.

Analysis of covariance within each species and submersion/emersion condition revealed that temperature had a significant ( $P < 0.05$ ) effect on the regression coefficients. Temperatures with significantly different coefficients are shown with an asterisk (\*) in Tables 1 and 2. The results were then corrected to a specific weight by species, size class, temperature, and submersion/emersion condition (see METHODS) for comparison.

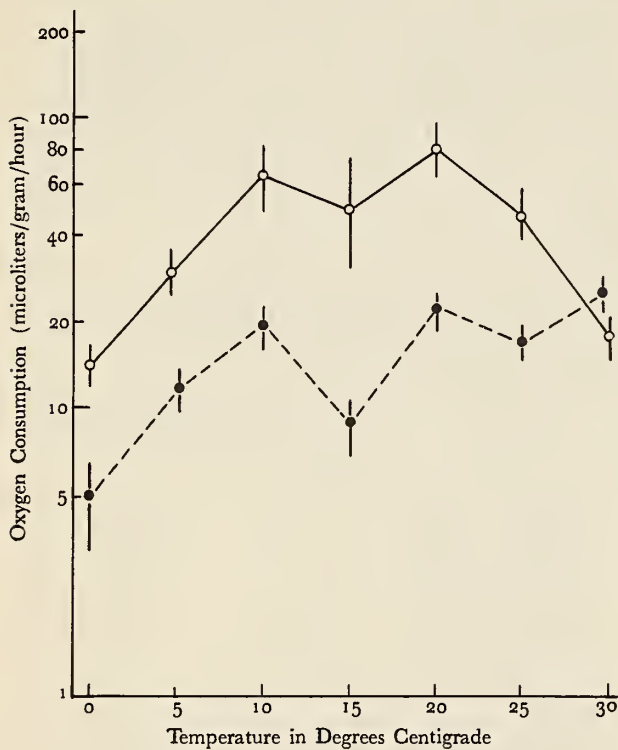


Figure 4

Emerged respiration for large (●) and small (○) size classes of *Thais lamellosa*. Each point represents at least 17 individual rates that have been weight-corrected (see Methods) and averaged. Vertical bars indicate 95% confidence intervals

The acute R-T curves for emerged large and small *Thais lamellosa* (Figure 4) show similar patterns with some important differences. Below 10°C both size classes are temperature dependent. Above this temperature the small *Th. lamellosa* show no significant increases in meta-

bolism with increasing temperature as would be expected if the rates were following the principle of Arrhenius (PROSSER, 1973). The larger snails (Figure 4), however, show significant ( $P < 0.05$ , ANOVA) increases with temperature in both the 15 to 20°C and 25 to 30°C ranges.

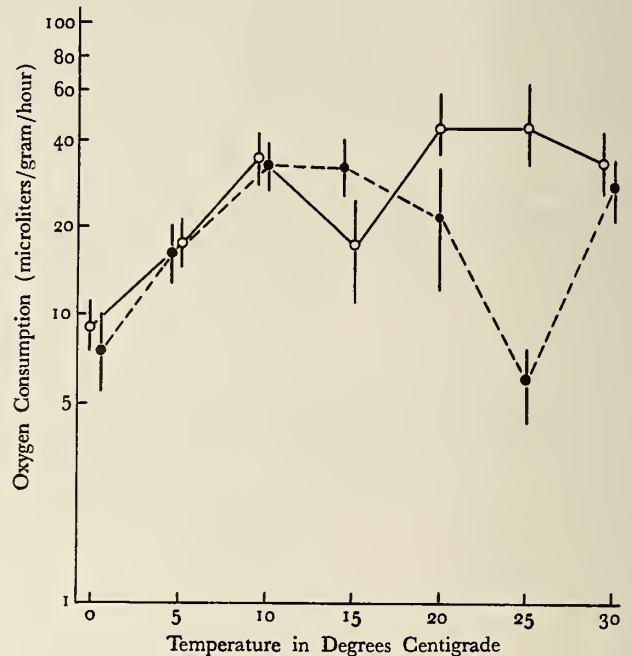


Figure 5

Emerged respiration for large (●) and small (○) size classes of *Thais emarginata*. Each point represents at least 17 individual rates that have been weight-corrected (see Methods) and averaged. Vertical bars indicate 95% confidence intervals

The metabolic rate/temperature curves for the emerged size classes of *Thais emarginata* (Figure 5) are also temperature dependent below 10°C. The small *Th. emarginata* show temperature independence above 10°C (except for a significant drop and subsequent rise in metabolism around the 15°C acclimation temperature). The large *Th. emarginata* (Figure 5) show a steady decline from 10 to 25°C followed by a sharp and significant increase ( $P < 0.05$ , ANOVA) from 25 to 30°C.

The submerged R-T curves for *Thais emarginata* (Figure 6) show a temperature independent metabolism



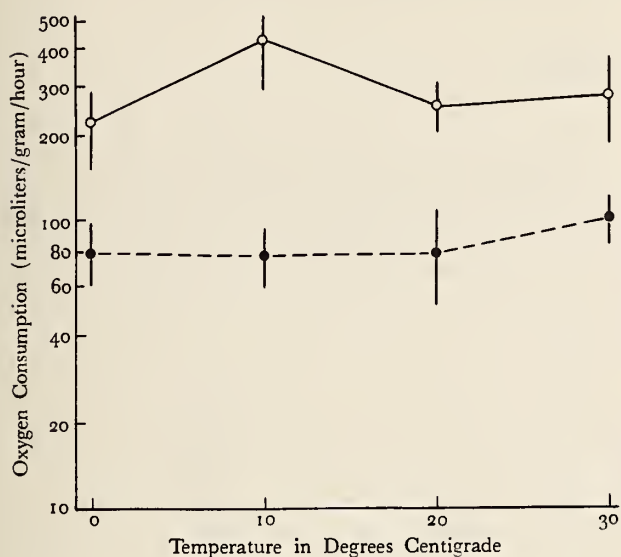


Figure 6

Submerged respiration for (●) and small (○) size classes of *Thais emarginata*. Each point represents 8 individual rates that have been weight-corrected (see Methods) and averaged. Vertical bars indicate 95% confidence intervals

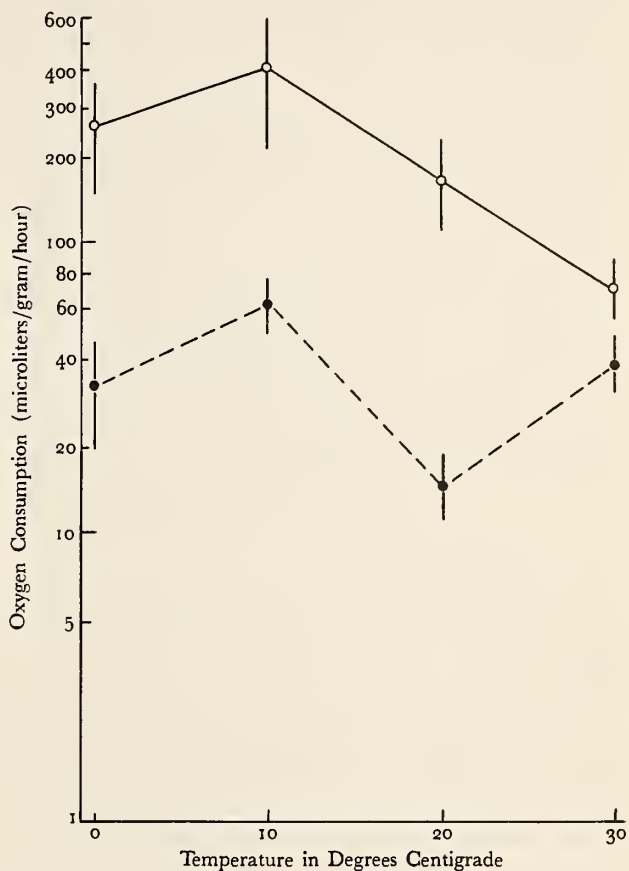


Figure 7

Submerged respiration for (●) and small (○) size classes of *Thais lamellosa*. Each point represents 8 individual rates that have been weight-corrected (see Methods) and averaged. Vertical bars indicate 95% confidence intervals

for both size classes ( $P < 0.05$ , ANOVA). In *Th. lamellosa* (Figure 7), the small size class shows no significant increase in metabolism with increasing temperature, whereas the large size class shows significant temperature dependence between 0 to 10°C and 20 to 30°C intervals.

Temperature independence of metabolic rates found in intertidal organisms has been shown to be an attribute of standard metabolism (NEWELL, 1969). Since the techniques used to separate active and standard metabolism (NEWELL & NORTHCROFT, 1967) are complex, this distinction was not made. The lack of statistical difference between metabolic rates at different temperatures would appear to be just as valid a reason for assuming temperature independence. This reasoning is particularly sound for emerged thaidis which when out of water are relatively inactive (see below). The general low rate of activity in the thaidis (Figures 8 and 9) would suggest that the results roughly represent standard metabolism and therefore support the conclusions of NEWELL (*op. cit.*).

The 2 thaidis under consideration appear to be adapted to an intertidal existence with varying degrees of tempera-

ture-independent metabolic rates. NEWELL (1969) gives examples of subtidal species that show no temperature independence in contrast to the many intertidal species that do. The implication here is that the adaptive value and occurrence of temperature independent metabolisms will increase with increasing tidal height. The data presented in this paper agree with this prediction. In both species a trend is seen towards greater temperature independence in the smaller individuals. Since the smaller individuals of both species are found higher on the beach (BERTNESS, 1976), this could represent a metabolic adaptation for the size gradient distribution. In addition, the

higher intertidal *Thais emarginata* (CONNELL, 1970) shows more temperature independence than *Th. lamellosa*. This is especially evident in the comparison of the submerged R-T curves (Figures 6 and 7).

The intraspecific differences seen in the R-T curves (Figures 4 - 7) appear to be most pronounced at the high end of the temperature range (25 to 30°C). With the exception of the submerged *Thais emarginata* which show complete statistical temperature independence, the large size classes show increased respiratory rates over this range while the small size classes show decreases. Since the shore-level size gradient found in both species finds the large snails in the more thermally stable environment in relation to the smaller individuals, this divergence between the respiratory responses of large and small sizes could be reflecting physiological adaptation. These increases in metabolic rate at high temperatures in the large size classes could be indicative of a metabolism that is out of control, *i. e.*, has lost the ability to regulate its respiratory rate at high temperatures, and could be an indication of heat coma or approaching thermal death. This is supported in *Th. lamellosa* where the lethal thermal limits of the large size class was found to be lower than for smaller snails.

Both thaidis were found to have significantly higher ( $P < 0.05$ , ANOVA) respiratory rates while submerged than when emerged. Other authors (SANDISON, 1968; BANNISTER, 1974) have found just the opposite to be the case in a number of intertidal gastropods. A possible explanation for this could be that the majority of the snails on which the data are available are supralittoral littorines and limpets that spend as much or even more time out of as in the water. In regards to the effect of zonation on the respiratory rate, BANNISTER (1974) found that in *Patella lusitanica* the emerged rate was 3 times that of the submerged, while in the lower intertidal *P. caerula* the difference was considerably less (emerged twice that of submerged). Since the thaidis do not feed while emerged, a higher respiratory rate while exposed would be energetically wasteful. In the supralittoral snails exposed to air as much as water, it might not be possible to reduce respiration due to the length of exposure. Considering the zonation differences between and within *Thais lamellosa* and *Th. emarginata* populations, the same trend with zonation is evident. The percent increase in respiratory rate (from emerged to submerged conditions) for *Th. emarginata* ( $\bar{X} = 736.9\%$ ) is significantly higher ( $P < 0.05$ , paired t-test) than that of *Th. lamellosa* ( $\bar{X} = 371.3\%$ ). Within the size classes of each species, small *Th. emarginata* ( $\bar{X} = 1100.3\%$ ) show a significantly greater ( $P < 0.05$ , paired t-test) increases than the large snails ( $\bar{X} = 373.5\%$ ). A similar trend was seen in the size classes of

*Th. lamellosa* (small 670.7%, large 71.9%), but the difference was not significant ( $P < 0.10$ , paired t-test).

### Activity

The rate of activity of marine organisms has been investigated by studying cirral activity in barnacles (SOUTHWARD, 1964), and general mobility in many species (see NEWELL, 1970 for review). In these studies, activity has been investigated in relationship to acclimation patterns,

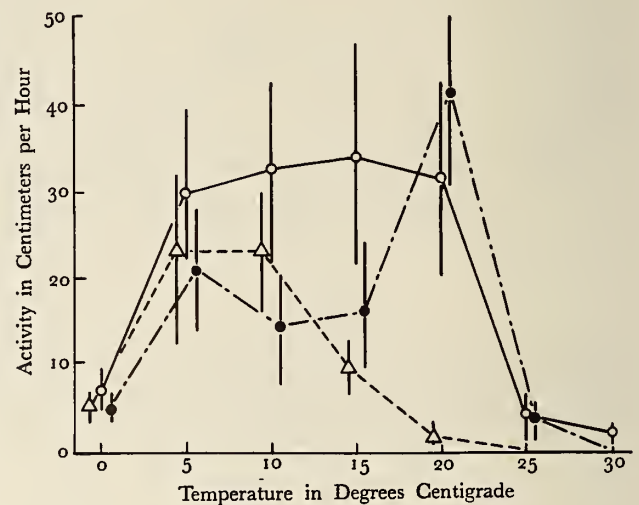


Figure 8

Submerged activity (rate of crawling) for large ( $\Delta$ ,  $3.98 \pm 0.284$  cm) and small ( $\bullet$ ,  $2.31 \pm 0.457$  cm) size classes of *Thais lamellosa* and *Thais emarginata* ( $\circ$ ,  $2.21 \pm 0.476$  cm). The data were collected in July, 1974, and all groups were acclimated at 15°C for 24 hours. Vertical bars are the 95% confidence intervals. Activity rates were taken for all groups at 5°C intervals from 0-30°C, and when no point is shown, it indicates zero activity

the effect of activity on respiratory rates, and activity as a function of time available to an organism to feed in intertidal organisms. These investigations have shown that temperature fluctuations of relatively short duration exert a profound effect on the rate of activity (SOUTHWARD, *op. cit.*; FRY, 1947), but prolonged exposure to high or low temperatures results in the development of compensatory changes in the activity rates (NEWELL, *op. cit.*). In the present study the mobility of *Thais lamellosa* and *Th. emarginata* is considered as a reflection of the effect of

temperature on the general physiological state of the snails.

Submerged activity (Figure 8) over a 0 to 30° C range of *Thais emarginata* and small and large size classes of *Th. lamellosa* shows significant differences between the 3 groups. All 3 groups are relatively inactive at 0° C. Between 5° C and 20° C *Th. emarginata*'s activity is statistically ( $P < 0.05$ , ANOVA) temperature independent. Within this range, the *Th. lamellosa* size classes respond differently to the temperature changes. While the small *Th. lamellosa* activity does not differ significantly at any one temperature from *Th. emarginata* ( $P < 0.05$ , ANOVA), the large *Th. lamellosa* activity drops to a value not significantly greater than zero ( $P < 0.05$ , ANOVA) at 20° C. At 25° C both *Th. emarginata* and small *Th. lamellosa* show drastically reduced activity and at 30° C *Th. emarginata* is the only group showing activity.

Comparable results for the emerged thaids (Figure 9) show *Thais emarginata* exhibiting much more activity than either of the *Th. lamellosa* classes. Between the *Th.*

*lamellosa* size classes there is no difference ( $P < 0.05$ , ANOVA) in activity between 0 and 15° C, but at 20° C the small *Th. lamellosa* are still active in contrast to the large size class.

In regards to activity as a reflection of the general physiological response of the thaids to temperature variation, both submerged and emerged activity reflect the intertidal zonation and resulting habitat temperature regimes of the snails tested. Between the species the more exposed *Thais emarginata* display the widest range of activity, showing activity throughout the experimental temperature range. Intraspecifically the higher intertidal, small *Th. lamellosa* size class showed activity at higher temperatures after activity in the larger snails had ceased. Due to the fact that thaids are active predators in the intertidal zone, the effect of temperature on the rate of activity could have important ecological consequences, since foraging efficiency is probably directly proportional to the rate of movement.

## SUMMARY AND CONCLUSIONS

1. Populations of *Thais lamellosa* and *Th. emarginata* exhibit intraspecific shore-level size gradient patterns which place the smaller individuals at the top of each species vertical range. In addition, the *Th. emarginata* population is found higher in the intertidal zone than the *Th. lamellosa* population. On the basis of surface area to volume ratio considerations, the smaller thaids which are found in the most physically stressful portion of each species range would be expected to be the most vulnerable to physical stress.
2. The lethal thermal limits of the 2 thaids reveal inter- and intraspecific differences in their tolerances. The higher intertidal *Thais emarginata* show the greatest thermal resistance, and within the *Th. lamellosa* size classes the small snails have the highest thermal limits. Humidity is shown to be an important factor in the thermal limits and it is suggested that the smaller snails could possibly more effectively utilize evaporative cooling as a temperature regulating mechanism.
3. The respiratory response to temperature increase indicated that the higher intertidal *Thais emarginata* and the small size class within each species displayed the most pronounced temperature independence.
4. The highest temperatures at which *Thais emarginata* and small and large size classes of *Th. lamellosa* remain active, over a 0 - 30° C temperature range, correlate to their natural distribution and consequential temperature regimes of their habitats.

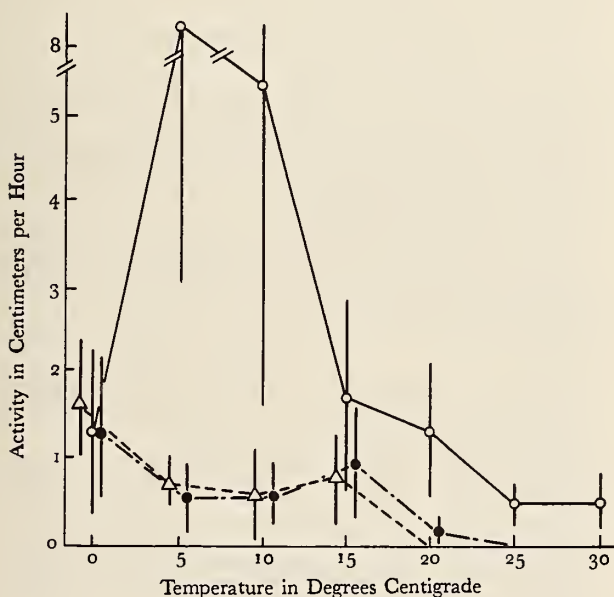


Figure 9

Emerg activity (rate of crawling) for large ( $\Delta$ ,  $4.21 \pm 0.126$  cm) and small ( $\bullet$ ,  $2.14 \pm 0.632$  cm) size classes of *Thais lamellosa* and *Thais emarginata* ( $\circ$ ,  $2.018 \pm 0.632$  cm). Vertical bars are the 95% confidence intervals. Activity rates were taken for all groups at 5° C intervals from 0 - 30° C, and when no point is shown, it indicates zero activity

5. Since both *Thais lamellosa* and *Th. emarginata* possess behavioral patterns, which establish and maintain their inter- and intra-specific zonation patterns (BERTNESS, 1976), the adaptations to thermal stress demonstrated in this paper probably do not play a major role in directly creating the observed distributional patterns. Rather, the physiological adaptations found allow the populations to exhibit their inter- and intra-specific zonation difference. The major effect of temperature stress on the thais probably does not result from direct mortality, but from the sublethal effects of high temperatures that can cause coma, increased metabolic rate, and reduced mobility. All of these factors potentially could have a detrimental effect on the competitive ability of the snails and therefore strengthen and reinforce the zonation patterns that are behaviorally established.

### Literature Cited

- BANISTER, J. V.  
1974. The respiration of air and water of the limpets *Patella caerulea* (L.) and *Patella lusitanica* (Gmelin). *Comp. Biochem. Physiol.* 49A: 407 - 411
- BERTNESS, MARK D.  
1976. Behavioral and ecological aspects of shore-level size gradients in *Thais lamellosa* and *Thais emarginata*. submitted to *Ecology*
- CONNELL, JOSEPH H.  
1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecol. Monogr.* 40 (1): 49 - 78; 9 figs. (Winter 1970)
- DAVIES, P. S.  
1966. Physiological ecology of *Patella*. I. The effect of body size and temperature on metabolic rate. *Journ. Mar. Biol. Assoc. U. K.* 46: 647 - 658  
1969. Physiological ecology of *Patella*. II. Desiccation effects. *Journ. Mar. Biol. Assoc. U. K.* 49: 291 - 304
- DAYTON, PAUL K.  
1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351 - 389
- EDWARDS, DALLAS CRAIG  
1969. Zonation by size as an adaptation for intertidal life in *Olivella biplicata*. *Amer. Zool.* 9: 399 - 417
- FINNEY, D. J.  
1971. Probit analysis. Cambridge Univ. Press, Cambridge, England, 333 pp.
- FRAENKEL, GOTTFRIED S.  
1960. Lethal high temperatures for three marine invertebrates: *Limulus polyphemus*, *Littorina littorea* and *Pagurus longicarpus*. *Oikos* 11 (2): 171 - 182
- FRY, F. E.  
1947. Effects of the environment on animal activity. *Univ. Toronto stud. biol.*, 55 (Publ. Ontario Fish. Res. Lab.) 68: 1 - 62
- GIBSON, J. S.  
1970. The function of the operculum of *Thais lapillus* in resisting desiccation and predation. *Journ. Anim. Ecol.* 39 (1): 159 - 168
- Gilson Medical Electronics  
1970. Operating instructions for the Gilson respirometer. Gilson Med. Electronics, Middleton, Wisconsin
- GREEN, E. J. & D. E. CARRITT  
1967. New tables for oxygen saturation of seawater. *Journ. Mar. Res.* 25 (2): 140 - 147
- HAMMEN, C. S.  
1969. Metabolism of the oyster, *Crassostrea virginica*. *Amer. Zool.* 9 (2): 309 - 318
- HARDIN, DAVID  
1968. A comparative study of lethal temperatures in the limpets *Acmaea scabra* and *Acmaea digitalis*. *The Veliger* 11 (Supplement): 83 - 87; 4 text figs. (15 July 1968)
- HEMMINGSSEN, AXEL M.  
1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rep. Steno. Mem. Hosp., Copenhagen* 9 (2): 7 - 110
- HOCHACHKA, PETER W. & T. MUSTAFA  
1972. Enzyme mechanisms and pathways in invertebrate facultative anaerobiosis. *Science* 176: 1056 - 1060
- KENSLER, C. B.  
1967. Desiccation resistance of intertidal crevice species as a factor in their zonation. *Journ. Anim. Ecol.* 36: 391 - 405
- LARSEN, M. J.  
1966. The influence of water temperature upon the life of the dogwhelk *Thais lapillus* (Gastropoda, Prosobranchia) *Journ. Anim. Ecol.* 35: 207 - 214
- LEWIS, JOHN B.  
1963. Environmental and tissue temperatures of some tropical intertidal animals. *Biol. Bull.* 124: 277 - 284
- MANCY, K. H. & W. C. WESTGARTH  
1961. The UNC galvanic cell oxygen analyzer. A spec. publ. of Dept. Engineering, School Publ. Health, Univ. No. Carolina, Chapel Hill, N. C.: 25 pp.
- MARKEL, R. P.  
1971. Temperature relations in two species of tropical West American littorines. *Ecology* 52 (6): 1126 - 1130
- MICALLEF, H.  
1966. The ecology and behaviour of selected intertidal gastropods. Ph. D. dissert., Univ. London
- MORTON, JOHN EDWARD, A. D. BONEY & E. D. S. CORNER  
1957. The adaptations of *Lasaea rubra* (Montagu), a small intertidal lamellibranch. *Journ. Mar. Biol. Assoc. U. K.* 36: 383 - 405
- NEWELL, RICHARD CHARLES  
1969. Effects of fluctuations in temperature on the metabolism of intertidal invertebrates. *Amer. Zool.* 9: 293 - 307  
1970. Biology of intertidal animals. vii + 555 pp.; 268 text figs. New York, Amer. Elsevier Co., Inc.
- NEWELL, R. C. & H. R. NORTHCROFT  
1967. A reinterpretation of the effect of temperature on the metabolism of certain marine invertebrates. *Journ. Zool. London* 151: 277 - 298
- PROSSER, CLIFFORD LADD  
1973. Comparative animal physiology. i - xxii + 456 pp.; illust. Philadelphia, Pa. (W. B. Saunders Co.)
- ROBERTS, J. L.  
1957. Thermal acclimation of metabolism in the crab *Pachygrapsus crassipes* Randall. I. The influence of body size, starvation, and molting. *Physiol. Zool.* (3): 232 - 242
- SANDISON, EYVOR E.  
1967. Respiratory response to temperature and temperature tolerance of some intertidal gastropods. *Journ. Exper. Mar. Biol. and Ecol.* 2: 271 - 281
- SOUTHWARD, A. J.  
1964. The relationship between temperature and rhythmic cirral activity in some Cirripedia considered in connection with their geographical distribution. *Helgol. Wissensch. Meeresunters.* 10: 391 - 403
- UMBREIT, W. W., R. H. BURRIS & J. F. STAUFFER  
1964. Manometric techniques. *Mpls. Minn. (Burgess Publ. Co.)* 253 pp.
- VERMEIJ, GEERAT J.  
1972. Intraspecific shore-level size gradients in intertidal molluscs. *Ecology* 53 (4): 693 - 700
- WOLCOTT, THOMAS G.  
1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at "limiting factors." *Biol. Bull.* 145 (2): 389 - 422